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Predation-Induced Changes in Growth Form in a Nudibranch-Hydroid Association

by

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Abstract. The estuarine hydroid *Cordylophora lacustris* was cultured under controlled laboratory conditions and several growth parameters were measured, including stolon growth rate, stolon budding rate, interstalk distance, and polyp budding rate. Young colonies of *C. lacustris* were subjected to experimental removal of polyps to determine whether physical and(or) chemical cues from predation by the nudibranch *Tenellia fuscata* induced any changes in growth form. Nudibranch predation and polyp removal with chemical stimuli from both direct and indirect exposure to nudibranch mucus caused decreased stolon growth rate and increased stolon budding. The result of these changes in growth should be a hydroid colony of greater density than without predation. Polyp removal without a chemical stimulus inhibited stolon budding, which would cause a more dispersed colony form. The results suggest that the hydroid responds differently to physical damage alone than to physical damage combined with the chemical stimulus of the mucus of its predator.

INTRODUCTION

NUDIBRANCH PREDATION on cnidarians has been documented numerous times and the feeding behavior of many nudibranchs described (see TODD, 1981). Less well known are defensive mechanisms utilized by their cnidarian prey. The defensive behaviors of a number of anemone species have been reported (ROSIN, 1969; HARRIS, 1973; EDMUNDS *et al.,* 1976; TODD, 1981), but little is known about possible responses by hydroids to nudibranch predation. Certainly nematocysts are released and polyps may contract, but are there any more subtle responses such as changes in growth form? Growth forms for a number of hydroid species have been described (see BRAVERMAN, 1974), but no studies to date have discussed the effect of predation on growth rate and form in a hydroid.

Herbivore attacks have been shown to induce changes in growth in plants (BOSCHER, 1979). HARVELL (1984) reported that nudibranch predation stimulated spine formation in the bryozoan *Membranipora membranacea* (Linnaeus, 1767), but no changes in growth form were observed. An arborescent hydroid might be expected to respond in one of three ways to a loss of tissues from nudibranch predation: (1) to grow slower with no change in colony form; (2) to grow more densely, paralleling the response of trees to pruning; and (3) to spread out the colony by elongation of stolons to "run away" from the predator.

The purpose of the present study is to determine whether nudibranch predation on the hydroid *Cordylophora lacustris* (Allman, 1844) would induce changes in growth form. *Cordylophora lacustris* is common in the euryhaline portions of rivers emptying into the Great Bay Estuary, and it is easily cultured under controlled laboratory conditions. The dendronotacean nudibranch *Tenellia fuscata* (Gould, 1870) is a natural predator of *C. lacustris* in the Great Bay Estuary and adapts well to laboratory conditions (HARRIS *et al.,* 1980). This study describes the results of short-term experiments testing for the effect of nudibranch predation on hydroid growth.

MATERIALS AND METHODS

The animals used in this study were collected from the Great Bay Estuary in New Hampshire and maintained in laboratory cultures in the Zoology Department of the University of New Hampshire. Colonies of the hydroid *Cordylophora lacustris* were collected from floats and pilings in the Lamprey River at Newmarket, New Hampshire, and both hydroids and the nudibranch *Tenellia fuscata* were obtained from floats in the Salmon Falls River at Stratham, New Hampshire.

Table 1

A summary of results of growth rate parameters measured under a series of control and experimental treatments testing for the effects of physical and chemical stimuli associated with polyp removal on growth rate in *Cordylophora lacustris*. The parameters measured were stolon growth (mm per day), stolon budding (buds per stolon per day), polyp budding (polyps per stolon per day), and interstalk distance (mm). The experimental treatments of polyp removal were (1) direct predation by *Tenellia fuscata* for 6 h, (2) removal of three polyps by forceps (no chemical stimulus), (3) removal of three polyps by forceps and rubbing a nudibranch over the wounds (direct chemical stimulus), and (4) removal of three polyps by forceps and presence of a nudibranch nearby but not in contact with the hydroid (indirect chemical stimulus). * Each experimental treatment differed from the control value to at least $P = 0.05$ level using ANOVA.

Growth parameters	Control	Direct feeding	Forceps only	Forceps & mucus (direct)	Forceps & mucus (indirect)	df	F-ratio	Significance
Stolon growth* (mm·day^{-1})	1.06	0.61	0.88	0.42	0.07	4/103	5.89	$P < 0.001$
Stolon budding* (buds·stolon^{-1}·day^{-1})	0.1	0.37	0.00	0.46	0.23	4/45	5.19	$P < 0.005$
Polyp budding (polyp·stolon^{-1}·day^{-1})	0.32	0.23	0.691	0.21	0.44	4/56	2.36	NS
Interstalk distance (mm)	3.25	3.04	3.0	2.61	2.76	4/42	0.43	NS

The hydroids were maintained in aerated aquaria at a constant temperature of 23°C and salinity of 20‰. Salinity was checked daily to eliminate the possibility that any changes in growth form were induced by abiotic factors. Experimental colonies were established by attaching fragments of colony containing stolon and one or two polyps to glass slides with nylon fishing line. The slides were suspended in an aquarium to which freshly hatched brine shrimp nauplii were added daily in order to maintain a constant food supply. Each slide was examined daily. Once a colony had attached and begun growing, it was utilized for one of several experiments.

Growth parameters in each colony were determined by placing the glass slide onto a plastic coated sheet of graph paper with a 1-mm^2 grid in a water-filled dish. The colony was then observed under a dissecting microscope and the colony was mapped on another piece of graph paper. All measurements were then made from the daily sequence of diagrams for each colony. Four growth parameters were consistently measured: (1) stolon growth rate; (2) stolon budding rate; (3) interstalk distance per stolon; and (4) polyp budding rate per stolon.

Tenellia fuscata was maintained in aquaria at the same temperature and salinity as the hydroids and fed colonies of *Cordylophora lacustris*. There were periods when a second hydroid, *Bougainvillea* sp., was used as food due to decreased availability of *C. lacustris*.

In order to determine the feeding rate of adult nudibranchs, specimens of *Tenellia fuscata* were allowed to feed on hydroid colonies of known size for 24 h. The number of polyps consumed was counted and an hourly polyp consumption rate was calculated. Nudibranchs were also allowed to feed on colonies for 6 h to verify the feeding rate. All experiments for growth responses to nudibranch predation in *Cordylophora lacustris* were based on this 6-h time period.

The impact of polyp removal on hydroid growth was tested using four variations. (1) A nudibranch was allowed to feed on a colony for 6 h and then removed. (2) Polyps were removed by forceps to mimic predation without a chemical stimulus. (3) Polyps were removed by forceps and then a nudibranch was rubbed over the wounds to mimic predation including a direct chemical stimulus. (4) Polyps were removed by forceps and the colonies were maintained in an aquarium where a nudibranch was held in a mesh container to provide only an indirect chemical stimulus. Regeneration rates of removed polyps were also monitored using the same four treatments.

All experiments involved three or more replicates per treatment and each experiment was run at least two times. Colonies were followed for approximately a week after the treatments. Analysis of variance was used to test for the statistical significance of various results in each experiment.

RESULTS

Growth rate measurements, made during the early phases of colony formation by newly attached fragments of colonies, are given in Table 1. Colony formation during the early stages of establishment on glass slides involves extensive stolon growth and limited upward growth of stalks, so that most stalks contain only one or two polyps. This pattern appears to change only after stolons begin to regularly overlap each other and most of the slide is colonized; then growth shifts to production of branching stalks containing many polyps.

Tenellia fuscata is an active and fast growing nudibranch (Harris *et al.*, 1980). Individual nudibranchs were seen feeding in two ways during observations to determine feeding rates. The most common method was for *Tenellia* to crawl up a hydroid stalk to the base of the polyp, grasp

it in the jaws, and rasp away tissue until the hydranth was consumed. Nudibranchs were also observed to make a hole in the perisarc of a stalk and to consume tissue and fluids by a combination of rasping and pumping movements of the radula and buccal mass. Direct consumption of polyps was the primary feeding method observed when nudibranchs were on growing hydroid colonies with an abundance of polyps. The mean feeding rate determined for 6- and 24-h tests was 0.48 polyp per hour or 11.52 polyps per day. In all experiments in which forceps were used to mimic predation, three polyps were removed to represent approximately 6 h of feeding by a nudibranch. All hydroid colonies used had been recently established on slides. Three polyps constituted a loss of no more than 10% of the polyps in a colony.

The most obvious change in growth following polyp removal was a decrease in stolon growth rate and a change in stolon budding rate (Table 1). Stolon growth rate might be expected to decrease along a stolon where polyps and, therefore, feeding capability were reduced. The increase in stolon budding may have accounted for the slowdown in stolon growth rate and represented a shift in growth form.

The decrease in stolon growth was least where no chemical stimulus from a nudibranch was present; stolon budding actually ceased in the portions of those colonies that were monitored. Stolon growth was least in colonies that were exposed to only indirect chemical cues, but the stolon budding rate did not change as dramatically as in the cases where mucus directly contacted the colonies. A major difference between treatments, though, was that in cases of direct mucus contact, the contact lasted no more than 6 h (direct predation) and often only a few minutes (forceps and mucus), while the colonies used in the indirect chemical stimulus tests remained in culture with a nudibranch for several days and were, therefore, presumably exposed to low levels of chemical stimulus for the duration of the experiment.

The different treatments caused decreased or increased rates of polyp budding. In the two cases where nudibranch mucus directly contacted the damaged portion of the colonies, polyp production decreased. In contrast, polyp production increased in the two tests where mucus was not present or was not in direct contact with the hydroid. Slight decreases in interstalk distance occurred along stolons where polyps were removed, but such changes did not correlate with decreases in stolon growth rates.

The net result of the observed responses to polyp removal was predicted to be a denser colony form with more stolon branching and decreased interstalk distance. The one exception may be where no chemical stimulus was present, because a continuation of the observed sharp decrease in stolon budding would produce a very diffuse colony form.

Cordylophora lacustris showed a consistent pattern of polyp regeneration following removal of several polyps (Table 2). Polyps regenerated in a sequential fashion along the stolon, beginning with the proximal or oldest polyp and progressing distally along the stolon. In all treatments, the regeneration rate of removed polyps was less than one polyp per day (Table 2), but this was faster than the polyp production rate for new polyps on a stolon. The quickest regeneration occurred in those polyps removed by nudibranch predation (Table 2), but the number of polyps that regenerated was small. The results were not statistically significant so they are at best suggestive that actual nudibranch predation of a polyp may affect the hydroid differently from removal by forceps.

Table 2

A summary of polyp regeneration rates and totals following the four methods of removal. Polyps were removed using the following treatments: (1) direct predation by *Tenellia fuscata,* (2) forceps alone, (3) forceps and application of nudibranch mucus, and (4) forceps and nudibranch in the same bowl but no direct contact.

Treatment	Regeneration rate (day^{-1})	Percent regenerated
Nudibranch predation	0.8	12.5
Forceps only	0.734	64.0
Forceps and mucus (direct)	0.429	68.0
Forceps and mucus	0.482	68.0

DISCUSSION

The growth form and rates of colony growth for *Cordylophora lacustris* are well studied (Fulton, 1961, 1962, 1963; Overton, 1963). Braverman (1974) has clearly documented the value of using hydroids for modeling growth in colonial organisms, plant and animal. Although it has been shown that herbivory can alter growth form in plants (Boscher, 1979), no similar work has been conducted on hydroids. The results of this study suggest that nudibranch predation does induce changes in rates of stolon growth and budding, which may alter growth form, and that there may be a chemical component involved in the induction process.

The colony morphology described in this study is similar to that reported for laboratory cultures of *Cordylophora lacustris* by previous workers (Fulton, 1961; Overton, 1963). Our stolon growth rate of 1.06 mm/day is slower than the approximately 3 mm/day reported by Fulton (1963), but the interstalk distances of about 3 mm were the same, suggesting that while growth form was similar, growth rate was about one-third the maximum rate achieved by Fulton (1963). The culture techniques we used could certainly have been refined, but our primary concern was in determining whether nudibranch predation affected growth rates and(or) form. Therefore, once we determined that our culture techniques produced healthy colonies with a consistent growth form similar to that described in the literature, we focused our efforts on the experiments described.

The experiments showed that predation either by *Tenellia fuscata* or by polyp removal by forceps, accompanied by direct or indirect exposure to *T. fuscata* mucus, induced increased stolon budding rates. Enhanced stolon budding results in a denser colony form. This change could be caused by removal of three polyps, using forceps, and an application of mucus to the wounded portion of the colony lasting only a few minutes. In fact, removal by forceps and direct contact with mucus stimulated a greater response, lower stolon growth rate, and higher stolon budding rate than actual predation by a nudibranch. The greater impact on the hydroid may have resulted from the removal of three polyps in a minute or two rather than from a nudibranch feeding on the same number of polyps over a 6-h period. HARRIS & HOWE (1979) found that mucus from the nudibranch *Aeolidia papillosa* (Linnaeus, 1767) induced a behavioral response in its prey, the anemone *Anthopleura elegantissima* (Brandt, 1835), but this appears to be the first evidence of predator-induced growth changes in a cnidarian.

It is interesting that removal of polyps independent of a chemical stimulus had a negative impact on stolon budding and thus alters colony morphology in an opposite way to that induced by polyp removal accompanied by a chemical cue from the nudibranch predator. Polyp budding increased when forceps were used alone, but without stolon budding there would be only a higher density of polyps along non-branching stolons growing away from the point of colony initiation—similar to a hedgerow instead of a grove. One of us (Harris) had hypothesized that a hydroid might respond to predation by a nudibranch by sending out stolons to disperse the colony as occurred when forceps were used alone. However, the opposite occurred, suggesting that *C. lacustris* grows away from areas of abiotically caused injury, whereas predation induces a growth response that leads to a denser colony.

Tenellia fuscata has a short life-span of about 30 days (HARRIS *et al.*, 1980). A single individual, even if it were able to feed at the maximum rate for its entire life-span, would consume less than 360 polyps. FULTON (1962) reported that a *Cordylophora lacustris* polyp might live more than 100 days and his colonies, in limited space, produced well over 2000 polyps. Therefore, a healthy colony could easily survive limited nudibranch predation, but would be swamped by numerous individuals as described by CHAMBERS (1943). A denser colony form induced by nudibranch predation may benefit the hydroid by making it more difficult for larvae, including the veligers of *T. fuscata,* to pass through the canopy of predatory polyps to settle within the colony. STANDING (1976) reported that *Obelia* sp. inhibited barnacle settlement by eating settling cyprids, thereby prolonging the persistence of the colony in the community. However, limited predation might have a positive effect on a hydroid as has been suggested for some host-parasite associations (CHENG, 1971; LINCICOME, 1971).

In conclusion, the predator-prey association between *Tenellia fuscata* and *Cordylophora lacustris* is more complex than the simple physical act of polyp removal by the nudibranch. It is a dynamic process involving rates of polyp addition and replacement to counter their loss through predation and changes in growth form induced by both physical damage as well as the combination of physical and chemical stimuli. The fact that both species adapt well to laboratory culture suggests that this system could be useful for studies relating to (1) chemical induction and (2) the dynamics of predator-prey associations.

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